Revista Chilena de Historia Natural
66: 283-289, 1993

Detritivores of the Chilean arid zone (27-32°S) and the Namib Desert: a preliminary comparison

Detritivoros de la zona árida de Chile (27-32°S) y del desierto de Namibia: una comparación preliminar

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ABSTRACT

In this review, the available literature and the wide field experience of the authors contribute to a comparison of the detritivores of the Chilean arid Zone (27-32°S) and the Namib Desert. Both regions, despite being on separate continents, have broad geographic and climatic similarities. They differ greatly, however, in age, physiography and biogeography. Earthworms are abundant in relatively moist parts of the Chilean Arid Zone (CAZ hereafter) that contain silty soil; they are absent in the Namib. Microarthropods associated with the decomposer food web are present in both regions, but may be better represented in the CAZ where mites, collembolans and psocopterans are abundant in soil and litter. Lepismatid thysanurans are very abundant in the Namib, but not so in the CAZ. Termites may be the most important detritivores in the Namib, where potentially detritivorous ants are also common in certain habitats. Neither of these social insects groups is well represented in the CAZ. Both regions are rich in species of tenebrionid beetles. Millipeds and crickets appear to play minor roles in detritus consumption in both regions.

Key words: Coastal deserts, Chilean Desert, Namib Desert, detritivores.

RESUMEN

La literatura disponible y la amplia experiencia de terreno de los autores permite, en esta revisión, comparar los organismos detritivoros de la región árida de Chile (32-27°S) y del desierto de Namibia. Ambas regiones, a pesar de estar en continentes separados, poseen amplias similaridades geográficas y climáticas. Ellas difieren, sin embargo, en edad, fisiografía y biogeografía. Las lombrices de tierra son abundantes en suelos limosos de los sectores relativamente húmedos de la zona árida chilena (ZAC en adelante); pero ausentes en el desierto de Namibia. Microartrópodos asociados a la trama trófica de la descomposición parecen estar mejor representados en la ZAC, donde psocópteros, ácaros y colémbolos son abundantes en el suelo y el mantillo. Tisanuros lepismátidos son muy abundantes en Namibia, pero no lo son tanto en la ZAC. Términes parecen ser importantes descomponedores en el desierto de Namibia, junto a hormigas en ciertos hábitat. Ninguno de estos grupos de insectos sociales está bien representado en la ZAC. Ambas regiones son ricas en especies de coleópteros tenebriónidos. Miriápodos y grillos no parecen importantes en ambas regiones.

Palabras claves: Desiertos costeros, desierto chileno, desierto de Namibia, detritivoros.

INTRODUCTION

The Chilean arid zone (hereafter referred to as the CAZ) is part of the narrow, coastal Desert found along the coastline of central South America. Its geographical counterpart in the Old World is the Namib Desert of southwestern Africa. Both are cool fog deserts near their respective coasts. Their interiors have great diel and annual temperature fluctuations. Aside from such broad climatic similarities, the CAZ and the Namib exhibit major differences in age and topography. These differences are reflected in the composition of their biotas.

Arid regions such as the CAZ and the Namib have very low levels of primary production (Rauh 1985, Hadley & Szarek 1981). Their brief and often irregular periods of plant growth are separated by long periods of drought (e.g., Walter 1973), when all ephemerals die (MK Seely, personal communication 1992) and persistent plants either reduce their living tissues or die (Evenari *et al.*

(Received 12 september 1992; accepted 4 January 1993.)

1982). This produces litter, or detritus, which is scattered and progressively fragmented by wind action. An unknown but possibly large fraction of the litter may also be degraded by ultraviolet radiation (Moorhead & Reynolds 1989, MacKay in press). What is not lost to physical forces becomes available to omnivorous animals called "detritivores" that typically dominate the animal biomass of deserts (Crawford 1991).

We use available literature as well as our own experience to compare the detritivores of the CAZ and Namib ecosystems. Such scavengers of particulate dead organic material (mostly plant litter) in terrestrial ecosystems are mainly arthropods. Gastropod molluscs and oligochaete annelids are also important detritus consumers in many land-based decomposer food webs. A wide range of detritivores other than oligochaetes typically inhabits deserts (Crawford 1981). Among vertebrates, the term "detritivore" has been applied to several species of desert lizards (Pietruszka *et al.* 1986) and may be appropriate for certain avian and mammalian scavengers as well.

In order to appreciate the distributions and roles of detritivores in the CAZ and the Namib, it is useful first to summarize the evolution and physical/biological attributes of these arid regions. Hence the following brief comparison is made of the two deserts.

THE DESERTS COMPARED

The CAZ is part the southern arid region of coastal South America that includes the Atacama and Peruvian Deserts to the north. The aridity that now characterizes this region may have begun in Holocene times (Ochsenius 1982, Arroyo *et al.* 1988), although some authors (cited by Rundel *et al.* 1991) feel that hyperadity has prevailed in northern Chile and southern Peru since the Middle to Late Miocene. The Namib, in contrast, appears to be much older and has probably been at least semi-arid for 80 million years (Ward *et al.* 1983). Both deserts now contain extensive regions of hyper-aridity and are generally considered among the driest places on earth.

Aridity in the CAZ and the Namib is maintained in part by the subsidence of dry tropical air (Lyndolph 1957, cited in Louw & Seely 1982; Trewartha 1961, cited in Rundel *et al.* 1991). Aridity is also promoted by the cold Humboldt and the cold Benguela upwelling Systems, which occur along the southwestern coasts a South America and Africa, respectively (Ward *et al.* 1983, Rauh 1985). Low temperatures generated by the currents condense moisture in landward-moving air, producing fogs that blanket coastal landscapes and dry air masses that pass to the interior. The fogs periodically extend inland due to offshore winds and coastal topography. Coastal fogs tend to be more seasonal (winter months) and subject to greater topographic relief in the CAZ than in the Namib (Louw & Seely 1982). Although other forms of precipitation are relatively unimportant along the coasts of both deserts, rainfall becomes increasingly significant, relative to fog, as one moves inland and/or gains elevation.

In a physiographic sense, the CAZ and the Namib are very different. An irregular range of low mountains (Cordillera de la Costa) rises abruptly along the coast of the former. Inversions of stratus clouds form thick, persistent fog banks that regularly cover the coastal scrub and lomas formations, as well as relict forests at higher elevations (Rauh 1985, Rundel *et al.* 1991). By comparison, most of the coastal Namib consists of extensive dunefields. These, like the coastal cordillera in Chile and Peru, are periodically shrouded in fog arriving from offshore. Although most Namib dunes are relatively free of vegetation, grasses and shrubs occur on their lower slopes and in interdunes (Seely 1978, Seely & Louw 1980).

The interiors of these two deserts also differ physiographically. The interior of the CAZ is characterized by an assortment of broad valleys and mixed landscapes. Human impacts in recent centuries have greatly altered the original vegetation. At present, the plant cover ranges from being virtually nonexistent to consisting of diverse communities that include many introduced species. Rain shadow effects created by the Andes greatly affect the climate and vegetation of the interior. To the east the valleys give way to a rocky, cactus-dominated desert, which merges with areas supporting thorn-shrubs and cushion plants as elevation increases. Eventually, one reaches the high altitude Puna Desert that extends to the upper limit of vegetation (Rauh 1985).

The interior of the Namib is quite unlike that of the CAZ. Much consists of extensive gravel plains, dominated by grasses that appear after rare rainfall events. The largely calcrete plains support conspicuous granitic, limestone and inselbergs and are dissected in places by dry river beds that cut through deep rocky gorges. These seaward-bound channels carry occasional runoff from the high escarpment at the Namib's eastern edge. Such water courses are usually lined by thin strips of acacia-dominated vegetation with understories of subtrees, shrubs and grasses. The overstory of this riparian community differs markedly from that of the CAZ, where more extensive woodlands of native and introduced trees border short rivers that run from the Andes to the Pacific. River and stream beds in both deserts, however, support shrub communities of remarkably similar architecture.

THE DETRITIVORES COMPARED

In light of the broad climatic similarities, as well as the probable great evolutionary differences and the obvious physiographic differences between the CAZ and the Namib, we now compare the detritivore faunas of the two deserts. In doing so, we confine our comments to taxa broadly acknowledged to play significant roles in decomposition. Groups that are primarily necrovores or coprovores are for the most part omitted from consideration.

Oligochaete Annelids

Earthworms and their relatives are seldom mentioned in the desert invertebrate literature. There is good reason for this: terrestrial annelids have a poor capacity to resist desiccation. In the Sahara Desert, however, a distinct earthworm fauna occupies both the fringes and habitats of the interior such as oases and higher elevations (El-Kifl & Ghabbour 1984). Species originating in regions to the south are considered endemic; others apparently arrived via several migration routes from Europe or were introduced by humans. In Egypt, several species are known to prefer clay soils but can be abundant in sandy soils when these are irrigated (Ghabbour 1977).

Earthworms are also abundant in the southernmost portions of the CAZ. We have observed their surface castings over kilometer-wide areas on hillsides and plains. Whether the species are introduced or native is unclear. We suggest two reason why they survive and fluorish in a region with less than 200 mm of annual rainfall. First, the irregular coastal fogs appear to maintain levels of soil moisture adequate for their survival, although this hypothesis should be tested. Second, the soils inhabited by the earthworms are silty and have relatively high moisture-holding capacities. Soils in the Namib coastal region are sandy and contain insufficient organic matter to support earthworms.

Microarthropods

Microarthropods directly or indirectly associated with the decomposer food web are not well known from the Namib. Oribatid and other mites as well as psocopteran insects have been extracted from leaf litter in the Kuiseb riparian gallery forest (Coineanu & Seely 1983, JA Wallwork personal communication 1992).

Species of hypogastrurid isotomid and neanurid collembolans are known to occupy the aerial interstitial medium of fine sand in the Namib (Thibaud & Massoud 1988).

Much more is known about similar microarthropods in the CAZ, where most studies have been done in north-central Chile (26°-32°S), a transitional belt between the hyperarid desert and semiarid central Chile. The microarthropod fauna there is dominated by mites and psocopterans (Covarrubias *et al.* 1964, Di Castri & Vitali-Di Castri 1971, Cepeda-Pizarro *et al.* 1993). Among the mites, prostigmatids and oribatids are the most common taxa, with the former ranking first. Changes in topography as well as canopy and litter quality play an important role in determining the density and diversity of soil mesofauna (Covarrubias *et al.* 1964, Covarrubias 1987, Cepeda *et al.* 1992). In mesic soils (e.g., relict habitats such as bottoms of small canyons or patches of mediterranean matorral) the fauna becomes enriched with collembolans and other minor groups (Saiz 1963, Di Castri & Vitali-Di Castri 1981).

In general, the mean density of species of CAZ soil and litter microarthropods is cor-

related with the degree of structural complexity of the corresponding plant communities (Covarrubias *et al.* 1976, Di Castri & Vitali-Di Castri 1981). Temporal changes in density and diversity appear to be inversely correlated with this structural hierarchy (Covarrubias *et al.* 1976). Irrigated soils in the coastal steppe show a higher mean density of microarthopods than do natural soils in the same area. Acaridid mites tend to have higher populations than prostigmatid mites in irrigated soils.

Millipedes

The order Spirostreptida contains the most obvious millipedes in arid regions (Crawford 1979). In the Namib, these often large-bodied detritivores become active around inselbergs (Crawford & McClain 1983) and along normally dry water courses after rains. Species of harpagophorid spirostreptids may be locally important in such habitats but are certainly not as widespread in the Namib as they are in some other deserts (Crawford *et al.* 1987). Polydesmid millipedes are found in relict forests of the coastal CAZ; their distribution in non-forested areas has received little study.

Apterygote insects other than Collembola

At least forty species of lepismatid thysanurans inhabit the Namib Desert; about nine occur in the main dunefield (Watson & Irish 1988). Little is known of the ecology of the species that inhabit the non-dune environment, except that, like other desert lepismatids (Kaplin 1978), they consume detritus and live for up to five years. Dunefield species either occupy slipface or vegetation clump habitats (Watson 1989) and exhibit specific diel activity periods (Watson & Irish 1988). These small arthropods were abundant at a site that had earlier experienced an unusually strong rainfall event (Crawford & Seely 1987).

Lepismatid also occur in the CAZ and, like collembolans, are found in mesic soils in small canyons and patches of matorral (Saiz 1963, Di Castri & Vitali-Di castri 1981). Meinertellid microcorhyphians are also in the CAZ, but little is known about the species diversity or ecology of this group (Covarrubias *et al.* 1964).

Orthopteroid insects other than termites

To our knowledge there is little evidence that species in this category other than crickets, which are essentially omnivores, are significant detritivores either in the CAZ or in the Namib.

Termites

Termites are abundant throughout the world (MacKay 1991). They are important consumers of dead (and sometimes living) organic throughout southern Africa; 18 species in nine genera were reported by Coaton & Sheasby (1972) to inhabit what is now Namibia. Grass harvesters (e.g., *Trinervitermes*, some species of which build large mounds) and subterranean species (e.g., *Microcerotermes*) are members of the family Termitidae that occur in the Namib interior. The widespread hodotermitid, *Hodotermes mossambicus*, is a harvester common to both the interior and to portions of the dunefield. Also widespread is the rhinotermitid, *Psammotermes allocerus*, a subterranean species with galleries that extend to dune crest; it may well be the major consumer of detritus in the dunefield (Crawford & Seely unpublished results). At least one species of the kalotermitid genus *Epicalotermes*, which has colonies in dead wood not in contact with the ground, occurs in dry steam beds of the coastal region (Coaton & Sheasby 1972).

In contrast, termites appear to be inconsequential consumers in the CAZ (Covarrubias *et al.* 1964, Di Castri & Vitali-Di Castri 1981) and are apparently absent in most areas (personal observations).

Ants

Ants are usually abundant in deserts, both in term of numbers and species (MacKay 1991). They are opportunistic organisms, which may explain why many species survive in arid regions where food resources can be lacking in quality and quantity. The Namib appears to be relatively rich with 26 species (Marsh 1986). Ten species are granivores, ten are honeydew/nectar feeders, three are insectivores and three are omnivores. Few species are actually found in the dunefields. Their potential role as detritivores is not clear, although several are

seed harvesters. Their potential for moving dead organic material should be investigated.

On the other hand, the Chilean ant fauna is a depauperate derivative of the South American fauna (Snelling & Hunt 1975). Chile can be considered an "island" (Goetsch 1931); species have invaded from Peru and have also dispersed across the Andes. The hyperarid desert appears to be devoid of ants. The arid steppes are characterized by a distinctive, although not abundant fauna. The ubiquitous *Dorymyrmex goetschi* is the dominant ant of CAZ region and can be readily seen foraging in many habitats. Other species are occasionally seen in the CAZ; however, species which are common in more mesic areas are rarely found in the CAZ, except on the edges of relatively mesic habitats.

Large numbers of seed producing plants in the CAZ appear to exploited by only *Solenopsis gayi*. Althought the genus *Pogonomyrmex* is represented in Chile by five species of presumed seed harvesters, they are conspicuously absent in the CAZ. Numerous species of *Pogonomyrmex* are found in the arid zones of Argentina and in the deserts of North America.

Tenebrionid beetles

Tenebrionid beetles comprise an important part of the fauna in the CAZ and the Namib, as they do in many of the world's arid regions (Crawford 1981). Some species exhibit a degree of morphological convergence in both deserts, even though they are of different lineages. Forty one species are known from the central Namib dunefield. Of these, 60% (and 10% of their genera) are endemic to the region (Holm & Scholtz 1980). About half of them are day-active; in the absence of rain, individual abundances of these and night-active species are relatively low (Crawford & Seely 1987). However, after an unusually high rainfall event (118 mm) the detritivore biomass (mainly of tenebrionid beetles) increased by at least an order of magnitude, depending on the dunefield habitat; the increase was distinctly more rapid than that of the carnivore and herbivore biomass (Seely & Louw 1980). Some Namib dunefield tenebrionids (e.g., species of *Lepidochora* and *Onymacris*) are highly specialized for trapping fog water and for exploiting their dune habitats in unique ways (Seely 1978, 1983). Tenebrionids in the other Namib environments also range greatly in their adaptations to the great variety of habitats (Seely 1987).

Although the taxonomic status of the Tenebrionidae in the CAZ is still incomplete (Peña 1966, 1980), the fauna there is also diverse (Saiz & Vásquez 1980, Cepeda-Pizarro 1989) and comprises a significant portion of the food resources of local carnivores (e.g., ants, lizards, egrets, raptors and foxes). Most species are active in daylight and after high rainfall events. Some of them (e.g., the genera *Gyriosomus*, *Entomochilus* and *Nyctopetus*) are extraordinarily abundant and make up a large fraction of the total biomass of epigeic arthropods. One of the most typical species of arid north-central Chile is *Gyriosomas luczoti*, the density of which is strongly seasonally and rainfall dependent (Cepeda-Pizarro 1989). Studies in progress suggest that tenebrionids are important detritivores in the CAZ.

DISCUSSION

We have shown in this paper that the CAZ and the Namib Desert are roughly similar in geography and climate, yet very dissimilar in age and physiography. These differences, when coupled with tectonic effects that virtually eliminated intercontinental biotic exchanges after the late Mesozoic, appear to have produced strikingly different detritivore faunas in the two arid regions. In particular, earthworms are numerous in at least the more mesic parts of the CAZ but are absent in the Namib, while termites and ants are dominant in much of the Namib but are relatively scarce in the CAZ. Microarthropods (especially prostigmatid and oribatid mites, collembolans and psocopterans) associated with the decomposer food web are comparatively species rich and numerically abundant in the CAZ but, as far as we know, are depauperate in the Namib.

Differences may be less pronounced among the apterygote insects and the less dominant macrodetritivores. For example, lepismatid thysanurans are well documented detritivores in the Namib and may be fairly widespread in the CAZ. Again, spirostreptid millipedes are locally evident after rains in the Namib; poly-

desmid millipedes perhaps function in mesic parts of the the CAZ. Crickets may also be minor detritivores in the two regions.

Tenebrionid beetles are the most conspicuous shared element among the detritivore faunas of the CAZ and the Namib, despite their separate evolution on the continents concerned. Tenebrionids remain significant members of the worldwide community of desert detritivores (Crawford 1981).

To summarize the essential points in this paper, we find that plant litter in the comparatively young CAZ, which is bounded on the east by the Andes and on the north by additional desert, is mainly consumed by microarthropods and tenebrionid beetles, and in places by earthworms as well. In contrast, detritus in the much older Namib, with its lower eastern escarpment and more mesic northern border, in mainly processed by termites and ants, and also by tenebrionids. These are the broad patterns we presently discern among detritivores in the Chilean Arid Zone and the Namib Desert.

ACKNOWLEDGMENTS

We thank Julio Gutiérrez and Walter Whitford for organizing the La Serena International Workshop that led to this manuscript, and the University of La Serena for its hospitality during the meeting. Many individuals have contributed knowledge and ideas to what we have written; Mary Seely and Walter Whitford stand out among them. We acknowledge past support from our respective universities, and from the National Science Foundation (USA), the Foundation for Research Development of the CSIR (South Africa) and the Directorate of Nature Conservation and Recreation Resorts (Namibia).

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